



# Modification of the SPUR rangeland model to simulate species composition and pasture productivity in humid temperate regions

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## Abstract

Plant, water, and soil components of the Simulation of Production and Utilization of Rangelands model (SPUR 2.4) were incorporated into the Integrated Farm System Model (IFSM 1.2) to represent the growth and competition of multiple plant species in pastures and their effects on pasture productivity and botanical composition in temperate climates. Developed for semi-arid rangelands, SPUR required major adjustment to represent temperate pastures adequately. In particular, the effects of soil moisture on root and shoot mortality and photosynthetic rates were adjusted to represent greater susceptibility of temperate plants to drought. Sensitivity analysis showed that predicted total shoot dry matter appeared most sensitive to photosynthesis and growth parameters in the spring, soil moisture parameters in the summer, and senescence parameters in autumn. Across all seasons, shoot dry matter appeared most sensitive to optimum photosynthetic temperatures, specific leaf area, start and end dates of senescence, maximum nitrogen concentration in live shoots, and a maximum shoot specific growth rate. The revised pasture model incorporated into IFSM was calibrated with 2002 field data from experimental pastures in central Pennsylvania, USA containing primarily orchard-grass (*Dactylis glomerata*) and white clover (*Trifolium repens*). Predictive accuracy of the model was then further evaluated by comparing 2003 data from the same pastures to simulated production. The integrated submodel predicted soil water content and dry matter

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production relatively well. It did not achieve a desired degree of accuracy in predicting the dynamics of botanical composition; however, adjustment of SPUR subroutines to allow variable maximum root:shoot ratios and competition for light and water may improve predictions. Further development and use of this integrated model can help researchers improve their understanding of temperate pasture systems, identify gaps in knowledge, and prioritize future research needs. Ultimately, the integrated model could provide more accurate assessment of the influence of management strategies on pasture productivity, animal production, and economics at the whole-farm scale.

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## 1. Introduction

To improve the quantity and seasonal distribution of biomass production in temperate pastures, contemporary graziers tend to encourage the dominance of relatively few forage species (Tivy, 1990). Recent research suggests that increased diversity of plant species or functional groups may increase the productivity, sustainability, and nutrient retention of temperate pastures (Hector et al., 1999; Bullock et al., 2001; Sanderson et al., 2004a). To explore the long-term economic and environmental benefits of greater plant diversity, we modified the Integrated Farm System Model (IFSM; Rotz et al., 1999) to represent the dynamics of multiple-species pastures and the influence of these dynamics on pasture productivity, botanical composition, hydrology, and soil nutrients in temperate climates.

The IFSM, a deterministic, process-based model, predicts effects of weather and management on hydrology and soil nutrient dynamics, forage and crop yields, harvest, handling and feeding of crops, milk or beef production, manure management, and farm economics in temperate regions at a whole-farm scale. To simulate pasture plant dynamics, the current IFSM used modified portions of the grazing simulation model GRASIM (Mohtar et al., 1997), which itself had adapted the grass growth submodel of the Hurley Pasture Model (Johnson et al., 1983; Thornley, 1998) and the soil nitrogen dynamics of the Nitrate Leaching and Economic Analysis Package (NLEAP) model (Shaffer et al., 1991). Although capable of predicting productivity and nutritive quality of temperate grass pastures, IFSM lacked the structure necessary to simulate changes in the botanical composition of grass pastures or to simulate multi-species pastures. In contrast, the Simulation of Production and Utilization of Rangelands (SPUR) model, designed to predict vegetation and beef cattle production in semi-arid rangelands, allowed explicit simulation of multiple plant species on several sites (Hanson et al., 1988). Deemed valid for simulation of species-specific shoot dry matter in rangelands (Hanson et al., 1987; Carlson and Thurow, 1996), the model seemed to provide a suitable framework and submodels for simulating multiple species in temperate pastures.

Others have used the SPUR model to predict forage production in temperate regions. Stout et al. (1990) used the original SPUR model to predict biomass production and animal weight gains in hill-land pastures of West Virginia, USA. They found that SPUR, once calibrated, predicted animal weight gains relatively well but failed to predict pasture biomass production accurately (Stout et al., 1990). Stout (1994) then evaluated use of the original SPUR model on northeastern US grasslands and found that it predicted orchardgrass (*Dactylis glomerata*) and switchgrass (*Panicum virgatum*) biomass with acceptable correlations to measured yields ( $R^2 = 0.48$  and  $0.70$ , respectively). Since the original release of SPUR, researchers have improved the model's accuracy and broadened its ability to represent ecosystem processes (Hanson et al., 1992; Carlson and Thurow, 1992; Foy, 1993; Carlson and Thurow, 1996; Foy et al., 1999; Pierson et al., 2001). Consequently, we decided to incorporate a recent version of SPUR (version 2.4; Foy et al., 1999) into IFSM and modify the assumptions and structure of relevant SPUR submodels to improve simulated dynamics of hydrology, soil nutrients, plant productivity, and botanical composition in temperate humid pastures.

## 2. Methods

### 2.1. Model development

Model development consisted of (1) selecting SPUR submodels (or portions thereof) and integrating them with corresponding IFSM submodels, (2) adjusting SPUR submodels to represent temperate ecosystems, and (3) modifying SPUR structure and assumptions to improve accuracy of biomass predictions, usually by making the mechanistic representation of plant physiology more complex. First, IFSM's pasture submodel was replaced with that of SPUR, which separates plant dry matter into pools representing carbon and nitrogen in live shoots, live roots, propagules, dead shoots, and dead roots. We retained, however, an IFSM submodel that predicts symbiotic nitrogen fixation in legume species, based on the symbiotic nitrogen fixation submodel of Wu and McGechan (1999). This submodel calculates daily nitrogen fixation by a legume species as a function of legume root biomass, nodule:root dry matter ratio, maximum specific nitrogen fixation rate, and multipliers that decrease the maximum fixation rate in response to soil temperature, moisture, and inorganic nitrogen content. This submodel was modified by adding an equation to decrease the nodule:root ratio as the amount of inorganic nitrogen fertilizer applied per year increased.

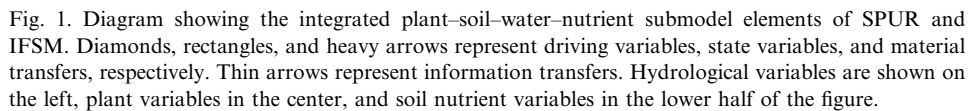
A set of user-defined parameters for each species simulated in SPUR determines the photosynthetic, mortality, germination, and uptake rates that influence changes in dry matter carbon and nitrogen pools. For the hydrology submodel, the IFSM calculations of runoff, actual evapotranspiration, and saturated soil water flow were replaced with SPUR equations. We also replaced IFSM's calculation of drained upper limit and lower limit of soil water by soil layer with user-specified values in SPUR's input file. We retained IFSM's methods of calculating potential

evapotranspiration (which appeared more accurate) and unsaturated soil water flow (which did not exist in the field-scale version of SPUR 2.4) (Jones et al., 1986). Integration with IFSM also prompted us to remove the influence of wind on the transfer of dead shoot biomass to the plant residue pool (IFSM's weather file lacks wind speed data) and to exclude SPUR's snowfall subroutines, which made all precipitation available in liquid form, as in IFSM.

Finally, SPUR's soil organic matter nitrogen state variables were added to IFSM's soil nutrient submodel. Although SPUR 2.4 allows representation of soil nutrients with a modified form of the CENTURY soil model (Parton et al., 1987; Foy et al., 1999), we chose to retain most of IFSM's simpler soil nutrient submodel for consistency with the soil nutrient submodels associated with crops in IFSM. These submodels, based on the NLEAP model, included state variables representing inorganic nitrate in shallow (0–30.5 cm) and deep (30.5–100 cm) soil layers, inorganic ammonium in the shallow soil layer, and organic carbon and nitrogen in soil organic matter and plant and manure residues. We retained an equation from IFSM that represents the spatial variability of feces and urine deposition by grazing cattle; it makes a proportion of inorganic soil nitrogen from manure unavailable to plants, though it remains available for loss through denitrification and leaching. Once combined, the integrated SPUR submodels represented the influences of weather and management on the dynamics of hydrology, soil nutrients, and dry matter of multiple plant species (Fig. 1).

Developed to predict dynamics in semi-arid rangelands with a single short growing season, SPUR required several modifications to plant-hydrology relationships to simulate temperate pastures. The most important of these changes included changing the lower limit of plant-extractable water in the soil from  $-5.0$  to  $-1.5$  MPa and, for a given mean soil water potential, increasing shoot and root mortality rates and decreasing transpiration and nitrogen uptake rates. Also, the influence of leaf age on photosynthetic rate was removed because repeated defoliation through grazing ensures that most leaves remain relatively young, even during late-season regrowth.

Finally, we made substantial modifications to SPUR structure to improve model accuracy and mechanistic representation of plant physiological processes. Dividing live shoot and live root carbon pools into structural and substrate components was the most significant change to the structure of the SPUR plant submodel; it allowed better representation of carbon dynamics such as photosynthesis, translocation, respiration, and structural growth. A multiplier of the photosynthetic rate was inserted from IFSM that equaled 0 (stops photosynthesis) if the proportion of shoot substrate exceeded 0.45 and then increased linearly to 1 (maximum photosynthetic rate) as the proportion of substrate decreased to 0.25. The proportion of substrate in shoots and roots was set to have direct influence on maintenance respiration (as in the Hurley Pasture Model) and structural growth rates (as in GRASIM). The desired shoot substrate proportion was set to 0.25, with excess shoot substrate translocated to roots. Following the lead of the Hurley Pasture Model, recycling of carbon from structural to substrate pools was added to represent translocation from senescing shoots (6%) and roots (3%) (Thornley, 1998).



We also adjusted how SPUR determined actual transpiration when too little soil water existed to meet potential transpiration demand. Originally, SPUR divided potential transpiration demand by soil layer as a function of root distribution ( $V_1$ ) and attempted to remove the calculated demand from each layer, starting with the top layer. If a soil layer contained too little water to meet its transpiration demand,

100% of unmet transpiration demand would cascade to the next lower layer, increasing the demand on that layer. Any unmet transpiration from that layer would transfer to the next lower layer; thus, cascading transpiration demand would continue to the lowest layer, if necessary. During simulated drought, this mechanism caused soil layers to dry to the lower limit of water content from the top layer down, including the lowest root-bearing layer (35–80 cm), which contained only a small percentage of total root biomass. To create a more realistic representation, we limited compensation of unmet transpiration demand by a given soil layer to 50%, instead of 100%, of the unmet demand of the soil layer above it. Cold adaptation was represented as stepwise increases in the minimum temperature for photosynthesis ( $P_5$ ) from  $-5$  to  $0$  °C during April and May of any year. The drought tolerance coefficient ( $P_7$ ), formerly user-defined in SPUR, was set equal to  $6.91/\ln(15/P_6)$  ( $P_6$  was mean water potential at which photosynthetic activity equals one-half maximum), an alternative equation in the model (Hanson and Skiles, 1987).

These changes made the complex SPUR model even more complex; however, they resolved many differences between simulation results and observations, revealing conceptual weaknesses in the SPUR 2.4 plant and soil subroutines when used to simulate humid temperate pastures. For example, dividing plant carbon into structural and substrate components greatly improved predictions of respiration (Cannell and Thornley, 2000) and dry matter dynamics. In addition, limiting transpiration demand as previously described greatly improved predictions of soil water content in deeper soil layers.

Weather data required by the pasture submodels were read from the IFSM weather data file, which included daily maximum and minimum temperature, precipitation, and downwelling solar radiation. Species-specific parameters related to plant physiology and initial dry matter state variables came from IFSM or a separate SPUR input file (Table 1). Site-specific parameters related to hydrology, soil physical characteristics, and soil nitrogen or carbon state variables and transformation rates also came from either IFSM or SPUR input files (Table 2).

## 2.2. Model calibration

The revised model was calibrated using dry matter and botanical composition data collected during the first year (2002) of a two-year dairy grazing study at Penn State University's John O. Almquist Research Center (DBRC), University Park, Pennsylvania, USA (Sanderson et al., 2004b). Twenty multiparous lactating dairy cows simultaneously grazed 0.9-ha pastures seeded in July 2001 with two replicates each of forage mixtures containing 2, 3, 6, or 9 species of grasses, legumes, and forbs. Cows grazed the pastures rotationally, grazing one replicate of a forage mixture in the morning and the mixture's second replicate in the afternoon of the same day. The only nitrogen applied to the pastures during the study came from feces and urine deposited by grazing cows. Plant data used from this study included botanical composition (e.g., grass, legume, weed, and dead components) and total live and dead shoot dry matter collected during three growth cycles each year: spring (mid to late April), summer (early to late July), and autumn (mid-September to mid-October).

Table 1

Species-specific parameters required to initialize the integrated SPUR submodel, their values by species, and sources of those values

Name	Definition	Units	Value		
			Orchardgrass	White clover	Cool-season forb (weed)
P <sub>1</sub>	Maximum photosynthetic rate	μmol CO <sub>2</sub> /m <sup>2</sup> /s	20.833 <sup>a</sup>	28.400 <sup>b</sup>	24.500 <sup>c</sup>
P <sub>2</sub>	Light-use efficiency coefficient	m <sup>2</sup> /W	2.000 <sup>d</sup>	1.300 <sup>d</sup>	1.300 <sup>d</sup>
P <sub>3</sub>	Maximum temperature for photosynthesis	°C	37.000 <sup>d</sup>	40.000 <sup>d</sup>	35.000 <sup>d</sup>
P <sub>4</sub>	Optimum temperature for photosynthesis	°C	21.000 <sup>f</sup>	29.500 <sup>a</sup>	21.000 <sup>c</sup>
P <sub>5</sub>	Minimum temperature for photosynthesis	°C	-5.000 <sup>b,j</sup>	-5.000 <sup>b,j</sup>	-5.000 <sup>b,j</sup>
P <sub>6</sub>	Mean soil water potential that halves photosynthetic rate	MPa	-0.500 <sup>e</sup>	-0.300 <sup>e</sup>	-0.800 <sup>e</sup>
P <sub>8</sub>	Proportion of photosynthate translocated to roots after senescence begins	None	0.100 <sup>e</sup>	0.100 <sup>e</sup>	0.100 <sup>e</sup>
P <sub>9</sub>	Maximum root:shoot ratio	None	5.000 <sup>b</sup>	5.000 <sup>b</sup>	4.000 <sup>d</sup>
P <sub>11</sub>	Precipitation tolerance coefficient	g/m <sup>2</sup> /cm	-0.400 <sup>d</sup>	-0.650 <sup>d</sup>	-0.650 <sup>d</sup>
P <sub>12</sub>	Proportion of phytomass susceptible to trampling	None	0.050 <sup>d</sup>	0.060 <sup>d</sup>	0.060 <sup>d</sup>
P <sub>13</sub>	Stocking rate tolerance of standing dead	ha/animal	-0.010 <sup>d</sup>	-0.010 <sup>d</sup>	-0.010 <sup>d</sup>
P <sub>14</sub>	Stocking rate tolerance of green shoots	ha/animal	-0.006 <sup>d</sup>	-0.006 <sup>d</sup>	-0.006 <sup>d</sup>
P <sub>15</sub>	Proportion of green shoots susceptible to death	None	0.004 <sup>d</sup>	0.005 <sup>d</sup>	0.005 <sup>d</sup>
P <sub>16</sub>	Specific leaf area	m <sup>2</sup> /g	0.035 <sup>b</sup>	0.035 <sup>b</sup>	0.035 <sup>b</sup>
P <sub>17</sub>	Proportion of photosynthate translocated to propagules after flower initiation	None	0.020 <sup>d</sup>	0.050 <sup>d</sup>	0.050 <sup>d</sup>
P <sub>18</sub>	Proportion of root phytomass translocated to shoots	None	0.005 <sup>d</sup>	0.005 <sup>d</sup>	0.005 <sup>d</sup>
P <sub>19</sub>	Germination proportion	None	0.010 <sup>d</sup>	0.005 <sup>d</sup>	0.005 <sup>d</sup>
P <sub>21</sub>	Proportion additional shoot death after senescence	None	0.020 <sup>e</sup>	0.020 <sup>e</sup>	0.020 <sup>e</sup>
P <sub>23</sub>	Seed mortality proportion	None	0.010 <sup>d</sup>	0.010 <sup>d</sup>	0.010 <sup>d</sup>
P <sub>24</sub>	Root and shoot respiration proportion	None	0.052 <sup>e</sup>	0.056 <sup>e</sup>	0.056 <sup>e</sup>
P <sub>25</sub>	Root mortality proportion	None	0.009 <sup>e</sup>	0.009 <sup>e</sup>	0.009 <sup>e</sup>
P <sub>28</sub>	Maximum nitrogen uptake coefficient	None	0.003 <sup>d</sup>	0.002 <sup>d</sup>	0.002 <sup>d</sup>
P <sub>29</sub>	Nitrogen use efficiency coefficient	m <sup>2</sup> /g	0.420 <sup>d</sup>	0.210 <sup>d</sup>	0.210 <sup>d</sup>
P <sub>30</sub>	Canopy-level light extinction coefficient	None	0.500 <sup>g</sup>	0.700 <sup>g</sup>	0.700 <sup>g</sup>
P <sub>31</sub>	Maximum symbiotic N fixation rate	mg N/day/g nodule	0.000	110.600 <sup>h</sup>	0.000
P <sub>32</sub>	Maximum proportion of shoot structure that photosynthesizes	None	0.800 <sup>e</sup>	0.800 <sup>e</sup>	0.800 <sup>e</sup>
CRIT <sub>1</sub>	Maximum leaf area index	None	8.000 <sup>f</sup>	6.000 <sup>e</sup>	6.000 <sup>e</sup>
CRIT <sub>2</sub>	Temperature for frost kill	°C	-6.000 <sup>d</sup>	-6.000 <sup>e</sup>	-6.000 <sup>e</sup>
CRIT <sub>3</sub>	Temperature for root translocation to shoot	°C	0.000 <sup>b</sup>	0.000 <sup>b</sup>	0.000 <sup>b</sup>
CRIT <sub>4</sub>	Minimum water potential for root translocation to shoot	MPa	-1.000 <sup>d</sup>	-0.800 <sup>d</sup>	-0.800 <sup>d</sup>
CRIT <sub>5</sub>	Minimum water potential for seed germination	MPa	-0.300 <sup>d</sup>	-0.300 <sup>d</sup>	-0.300 <sup>d</sup>
CRIT <sub>6</sub>	Day of year seed production begins	day of year	196.000 <sup>e</sup>	196.000 <sup>e</sup>	146.000 <sup>e</sup>
CRIT <sub>7</sub>	Day of year senescence begins	day of year	264.000 <sup>e</sup>	264.000 <sup>e</sup>	170.000 <sup>e</sup>

(continued on next page)

Table 1 (continued)

Name	Definition	Units	Value		
			Orchardgrass	White clover	Cool-season forb (weed)
CRIT <sub>8</sub>	Day of year senescence ends	day of year	285.000 <sup>e</sup>	285.000 <sup>e</sup>	235.000 <sup>e</sup>
RD	Maximum rooting depth	cm	80.000 <sup>f</sup>	80.000 <sup>i</sup>	15.000 <sup>e</sup>
PHYTM <sub>1</sub>	Initial live shoot dry matter	g/m <sup>2</sup>	5.000 <sup>e</sup>	10.000 <sup>e</sup>	5.000 <sup>e</sup>
PHYTM <sub>2</sub>	Initial live root dry matter	g/m <sup>2</sup>	300.000 <sup>b</sup>	300.000 <sup>b</sup>	150.000 <sup>b</sup>
PHYTM <sub>3</sub>	Initial propagule dry matter	g/m <sup>2</sup>	0.000 <sup>d</sup>	0.000 <sup>d</sup>	0.000 <sup>d</sup>
PHYTM <sub>4</sub>	Initial dead shoot dry matter	g/m <sup>2</sup>	4.000 <sup>e</sup>	4.000 <sup>e</sup>	4.000 <sup>e</sup>
CRITN	Maximum nitrogen concentration in live shoots	%	4.572 <sup>k</sup>	4.572 <sup>k</sup>	4.572 <sup>k</sup>
V <sub>1</sub>	Root distribution exponent	None	10.000 <sup>b</sup>	10.000 <sup>b</sup>	10.000 <sup>b</sup>
SMSGR	Shoot maximum specific growth rate	g/g/day	0.500 <sup>k</sup>	0.500 <sup>k</sup>	0.500 <sup>k</sup>
RMSGR	Root maximum specific growth rate	g/g/day	0.500 <sup>b</sup>	0.500 <sup>b</sup>	0.500 <sup>b</sup>
SMPS	Shoot minimum proportion substrate	None	0.050 <sup>b</sup>	0.050 <sup>b</sup>	0.050 <sup>b</sup>
RMPS	Root minimum proportion substrate	None	0.100 <sup>b</sup>	0.100 <sup>b</sup>	0.100 <sup>b</sup>
SSREC	Proportion of shoot structure recycled	None	0.060 <sup>l</sup>	0.060 <sup>l</sup>	0.060 <sup>l</sup>
RSREC	Proportion of root structure recycled	None	0.030 <sup>l</sup>	0.030 <sup>l</sup>	0.030 <sup>l</sup>
ETPGR	Minimum value for effect of temperature on structural growth	None	0.010 <sup>e</sup>	0.010 <sup>e</sup>	0.010 <sup>e</sup>
EMPPN	Minimum value for effect of soil moisture on photosynthesis	None	0.040 <sup>e</sup>	0.040 <sup>e</sup>	0.040 <sup>e</sup>
SUBGL	Desired shoot substrate proportion	None	0.250 <sup>e</sup>	0.250 <sup>e</sup>	0.250 <sup>e</sup>
FDBKCM	Proportion substrate at which photosynthesis stops	None	0.450 <sup>k</sup>	0.450 <sup>k</sup>	0.450 <sup>k</sup>

<sup>a</sup> Blaikie et al. (1988).<sup>b</sup> Skinner (co-author), pers. commun.<sup>c</sup> Bunce (2000).<sup>d</sup> Hanson and Skiles (1987).<sup>e</sup> Obtained through calibration.<sup>f</sup> Jung and Baker (1985).<sup>g</sup> Høgh-Jensen (1997).<sup>h</sup> Wu and McGeachan (1999).<sup>i</sup> Høgh-Jensen and Schjørring (1997).<sup>j</sup> Increases to 0 by the end of May each year.<sup>k</sup> from IFSM; decreases as live shoot biomass increases (Gastal and Lemaire, 2002).<sup>l</sup> Thornley (1998).



Table 2  
Site-specific parameters required to initialize the integrated IFSM-SPUR model and model sources of those values

Name	Definition	Units	Source	Value
C1	Watershed parameter representing slope and size relationships	h/ha	SPUR	7.413
C2	Watershed parameter representing climatic characteristics	None	SPUR	0.500
C5	Watershed parameter representing hydrograph shape	None	SPUR	4.000
CNI	Condition I curve number for site	None	IFSM <sup>a</sup>	62.900
USLEK	Soil erodibility factor for MUSLE	None	SPUR	0.320
USLEP	Erosion control practice factor for MUSLE	None	SPUR	1.000
USLEC	Cover/management factor for MUSLE	None	SPUR	0.090
USLESL	Slope-length factor for MUSLE	None	SPUR	0.024
CONA	Soil evaporation factor	mm/day <sup>0.5</sup>	IFSM	4.064
GR	Proportion of bare soil surface	None	SPUR	0.050
NMSL	Number of soil layers	None	SPUR	5.000
STF	Initial soil water content as proportion of drained upper limit	None	SPUR	1.000
BD	Moist bulk density of soil layers	g/m <sup>3</sup>	IFSM	1.250
SM0	Porosity of soil layers	cm/cm	IFSM <sup>a</sup>	0.528
SM3	Soil water content at drained upper limit (−0.033 MPa)	cm/cm	SPUR	0.325
SM15	Soil water content at lower limit (−1.5 MPa)	cm/cm	SPUR	0.110
SLSC	Saturated soil-hydraulic conductivity	cm/h	SPUR	4.800
ALB	Bare soil albedo	None	IFSM	0.120
SLDTH	Thickness of soil layers 1–5	cm	SPUR	3.0, 4.6, 7.6, 20.0, 45.0
SLT	Percent silt in soil	None	IFSM	48.000
CLY	Percent clay in soil	None	IFSM	27.000
NIT1	Initial inorganic nitrate in upper soil layer	kg/ha	IFSM	150.000
NIT2	Initial inorganic nitrate in lower soil layer	kg/ha	IFSM	50.000
NAF	Initial inorganic ammonium in upper soil layer	kg/ha	IFSM	0.000
RES	Initial plant litter dry matter	kg/ha	IFSM	2000.000
DROOTS	Dead root dry matter in soil	kg/ha	SPUR	5020.000
PNS <sub>1</sub>	Decomposition rate of dead root dry matter	kg/ha/day	SPUR	0.003
PNS <sub>3</sub>	Decomposition rate of soil organic matter	kg/ha/day	SPUR	0.00047
KDET	Rate of nitrate denitrification	kg/ha/day	IFSM	0.040
KMANR	Mineralization rate of organic manure residue nitrogen	kg/ha/day	IFSM	0.060
KRESR	Mineralization rate of organic plant residue nitrogen	kg/ha/day	IFSM	0.054
LCOEF	Soil leaching coefficient	None	IFSM	1.600
GRAZHA	Area of pasture	ha	IFSM	0.900
ANIMALS	Number of cows grazed	cows	IFSM	5.000
PNUNAVL	Proportion soil N unavailable to plants	None	IFSM	0.700

<sup>a</sup> Calculated in SPUR from IFSM input value.

Data for soil-particle size distribution and drained upper limit and lower limit water contents also came from DBRC. Daily maximum and minimum temperature, precipitation, and soil moisture data for 2002 and 2003 came from dataloggers at DBRC, except for the first 87 days of 2002 and the last 72 days of 2003, when air temperature and precipitation data came from a Penn State University automated surface observing system located at the Russell E. Larson Agricultural Research Center (LARC) in Rock Springs, Pennsylvania, ca. 12 km southwest of DBRC. Daily open-pan evaporation data from 2002, used to evaluate predictions of potential evapotranspiration, also came from this surface observing station at LARC. Daily downwelling solar radiation data for 2002 and 2003 came from a National Oceanic and Atmospheric Administration SURFRAD station, also at LARC.

The model was used to simulate only the “2-species” pastures at DBRC, which contained orchardgrass, white clover (*Trifolium repens*), and several weed species (e.g., dandelion (*Taraxacum officinale*), quackgrass (*Elytrigia repens*)), which we represented as a single cool-season forb, the dominant functional group of weeds in the 2-species pastures. Several species- and site-specific parameters were quantified using 2002 data from the field or relevant data from the literature (Tables 1 and 2). When lacking data to quantify a parameter, we either retained the default value supplied by IFSM or SPUR or adjusted the value during calibration. We used a preliminary sensitivity analysis (identical in method to the one described later, but differing in initial parameter values) to identify the parameters that most influenced predictions of shoot dry matter and soil moisture content. We focused on adjusting these parameters during model calibration (Wallach et al., 2001). To simulate the spring growth cycle, initial (1 Jan) shoot and root dry matter values were set to levels that placed predicted shoot dry matter at the beginning of the spring growth cycle (12 Apr) within the observed 95% confidence interval for shoot dry matter. For the summer and autumn growth cycles, which began immediately after grazing bouts, the model set total shoot dry matter equal to post-graze values observed in the field at the beginning of these 2002 growth cycles (2 Jul and 12 Sep) by decreasing shoot dry matter of all species by the same proportion. The most influential input parameters, identified with the preliminary sensitivity analysis, were adjusted iteratively until predicted soil moisture contents (at 13 and 61 cm) and total (live and dead) shoot dry matter had the best visual fits with corresponding 2002 field observations during spring, summer, and autumn growth cycles. We also ensured that model predictions of root dry matter, shoot and root nitrogen concentrations, shoot and root substrate carbon concentrations, biological nitrogen fixation, soil nitrogen availability and uptake, and evapotranspiration were within reasonable boundaries throughout the year.

### 2.3. Sensitivity analysis

Using the calibrated model (2002 weather), we evaluated the sensitivity of total shoot dry matter to independent changes in more than 60 species- and site-specific parameters (Tables 3 and 4). For each change in an input parameter, the relative change in total shoot dry matter was calculated at the end of each growth cycle in 2002 (30 Apr, 25 Jul, and 18 Oct) and at the end of the year (31 Dec). Following

Table 3

Sensitivity analysis index (*S*) of total live and dead shoot dry matter at the end of 2002 spring, summer, and autumn growth cycles and the end of the year for  $\pm 10\%$  and  $\pm 40\%$  changes in species-specific model parameters

Name	Definition	<i>S</i> by growth cycle							
		Spring		Summer		Autumn		End of year	
		$\pm 10\%$	$\pm 40\%$	$\pm 10\%$	$\pm 40\%$	$\pm 10\%$	$\pm 40\%$	$\pm 10\%$	$\pm 40\%$
P <sub>1</sub>	Maximum photosynthetic rate	0.40	0.35	0.07	0.08	-0.07	0.09	-0.77	-0.38
P <sub>2</sub>	Light-use efficiency coefficient	0.15	0.14	0.03	0.02	0.04	-0.03	-0.15	-0.26
P <sub>3</sub>	Maximum temperature for photosynthesis	<b>1.36</b>	<b>1.49<sup>a</sup></b>	0.00	0.23 <sup>a</sup>	0.38	0.53 <sup>a</sup>	<b>0.59</b>	<b>0.97<sup>a</sup></b>
P <sub>4</sub>	Optimum temperature for photosynthesis	<b>-1.97</b>	<b>-1.73</b>	0.00	-0.16	<b>-0.65</b>	<b>-0.64</b>	<b>-0.95</b>	<b>-1.01</b>
P <sub>5</sub>	Minimum temperature for photosynthesis	<b>-0.70</b>	<b>-1.25</b>	0.09	0.04	-0.09	-0.10	-0.07	-0.11
P <sub>6</sub>	Mean soil water potential that halves photosynthetic rate	0.00	0.00	<b>0.43</b>	<b>0.43</b>	0.36	0.33	-0.03	0.03
P <sub>8</sub>	Proportion of photosynthate translocated to roots after senescence begins	0.00	0.00	0.00	0.00	-0.05	-0.05	-0.05	-0.05
P <sub>9</sub>	Maximum root:shoot ratio	-0.49	-0.56	0.00	0.00	-0.01	-0.04	-0.13	-0.11
P <sub>11</sub>	Precipitation tolerance coefficient	-0.02	-0.02	-0.04	-0.04	-0.12	-0.13	<b>-0.71</b>	<b>-0.71</b>
P <sub>12</sub>	Proportion of phytomass susceptible to trampling	0.00	0.00	-0.01	-0.01	-0.01	-0.01	-0.01	-0.01
P <sub>13</sub>	Stocking rate tolerance of standing dead	0.00	0.00	-0.01	-0.01	-0.01	-0.01	-0.01	-0.01
P <sub>14</sub>	Stocking rate tolerance of green shoots	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01
P <sub>15</sub>	Proportion of green shoots susceptible to death	0.00	0.00	-0.01	-0.01	-0.03	-0.01	-0.02	-0.03
P <sub>16</sub>	Specific leaf area	0.21	0.23	<b>-0.48</b>	<b>-0.61</b>	<b>-0.48</b>	<b>-0.49</b>	-0.53	-0.54
P <sub>17</sub>	Proportion of photosynthate translocated to propagules after flower initiation	0.00	0.00	0.00	0.00	-0.02	-0.01	-0.02	-0.02
P <sub>18</sub>	Proportion of root phytomass translocated to shoots	-0.02	-0.01	0.01	0.01	0.01	-0.01	0.04	0.00
P <sub>19</sub>	Germination proportion	0.02	0.01	0.00	0.00	-0.01	0.00	-0.02	-0.01
P <sub>21</sub>	Proportion additional shoot death after senescence	0.00	0.00	-0.01	-0.01	-0.26	-0.27	<b>-0.88</b>	<b>-0.87</b>
P <sub>23</sub>	Seed mortality proportion	-0.01	-0.01	0.00	0.00	0.01	0.00	0.05	0.02
P <sub>24</sub>	Root and shoot respiration proportion	0.01	-0.02	0.00	0.00	-0.02	0.01	0.16	0.17
P <sub>25</sub>	Root mortality proportion	-0.03	-0.09	0.00	0.00	0.01	-0.02	0.11	0.05
P <sub>28</sub>	Maximum nitrogen uptake coefficient	0.03	0.13	0.02	0.02	0.17	0.18	0.06	0.27
P <sub>29</sub>	Nitrogen use efficiency coefficient	-0.02	-0.02	-0.01	-0.01	-0.04	-0.04	-0.08	-0.05
P <sub>30</sub>	Canopy-level light extinction coefficient	-0.03	-0.03	0.00	0.00	-0.03	0.00	0.03	0.04
P <sub>31</sub>	Maximum symbiotic N fixation rate	0.00	0.02	0.00	0.00	-0.02	0.01	-0.02	0.01

(continued on next page)

Table 3 (continued)

Name	Definition	<i>S</i> by growth cycle							
		Spring		Summer		Autumn		End of year	
		±10%	±40%	±10%	±40%	±10%	±40%	±10%	±40%
P <sub>32</sub>	Maximum proportion of shoot structure that photosynthesizes	0.00	0.00	<b>−1.14</b>	<b>−0.72</b>	−0.50	−0.28	−0.51	−0.32
CRIT <sub>1</sub>	Maximum leaf area index	0.00	0.00	0.01	0.00	0.00	0.02	−0.03	0.02
CRIT <sub>2</sub>	Temperature for frost kill	0.09	0.10	0.00	0.00	0.01	−0.01	0.14	0.05
CRIT <sub>4</sub>	Water potential for root translocation to shoot	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CRIT <sub>5</sub>	Water potential for seed germination	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CRIT <sub>6</sub>	Day of year seed production begins	0.00	0.00	0.01	0.01	0.00	0.01	−0.05	−0.03
CRIT <sub>7</sub>	Day of year senescence begins	0.00	0.03	0.04	0.16	<b>1.33</b>	<b>0.34</b>	<b>1.85</b>	<b>0.92</b>
CRIT <sub>8</sub>	Day of year senescence ends	0.00	0.00	<b>0.04</b>	<b>0.27</b>	<b>2.44</b>	<b>0.46</b>	<b>3.32</b>	<b>1.13</b>
CRITN	Maximum nitrogen concentration in live shoots	<b>−0.62</b>	<b>−0.63</b>	−0.03	−0.05	<b>−0.64</b>	<b>−0.44</b>	<b>−1.03</b>	<b>−0.69</b>
V <sub>1</sub>	Root distribution exponent	0.00	0.00	<b>−0.37</b>	<b>−0.44</b>	−0.10	−0.16	−0.01	0.02
RMSG <sub>R</sub>	Root maximum specific growth rate	0.00	−0.01	−0.01	−0.01	−0.01	0.00	−0.03	−0.01
SMSG <sub>R</sub>	Shoot maximum specific growth rate	<b>0.63</b>	<b>0.67</b>	<b>0.17</b>	<b>0.18</b>	<b>0.49</b>	<b>0.46</b>	0.70	0.69
SMPS	Shoot minimum proportion substrate	−0.13	−0.10	−0.05	−0.05	−0.12	−0.12	−0.17	−0.19
RMPS	Root minimum proportion substrate	0.00	0.01	0.01	0.01	−0.03	0.01	0.04	0.05
SSREC	Proportion of shoot structure recycled	0.03	0.01	0.00	0.00	0.01	0.01	0.06	0.04
ETPGR	Minimum value for effect of temperature on structural growth	0.02	0.03	0.00	0.00	0.06	0.01	0.06	0.02
PHYTM <sub>1</sub>	Initial live shoot biomass	0.21	0.20	−0.01	−0.02	0.04	0.02	0.04	0.00
PHYTM <sub>2</sub>	Initial live root biomass	<b>0.60</b>	<b>0.67</b>	−0.02	0.00	0.01	0.01	0.05	0.06
PHYTM <sub>4</sub>	Initial dead shoot biomass	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
SUBGL	Desired shoot substrate proportion	0.00	0.00	<b>0.46</b>	<b>0.46</b>	<b>0.70</b>	<b>0.63</b>	0.63	0.58
FDBKCM	Proportion substrate at which photosynthesis stops	<b>0.68</b>	<b>1.21</b>	−0.05	0.01	0.05	−0.03	0.03	−0.07

Values in bold indicate, by season, the seven species-specific parameters to which predictions appear most sensitive (see text for explanation of *S*).

<sup>a</sup> Decreased only by 30% to keep it higher than optimum photosynthetic temperature (P<sub>4</sub>).

Table 4

Sensitivity analysis index (*S*) of total live and dead shoot dry matter at the end of 2002 spring, summer, and autumn growth cycles and the end of the year for  $\pm 10\%$  and  $\pm 40\%$  changes in site-specific model parameters

Name	Definition	<i>S</i> by growth cycle							
		Spring		Summer		Autumn		End of year	
		$\pm 10\%$	$\pm 40\%$	$\pm 10\%$	$\pm 40\%$	$\pm 10\%$	$\pm 40\%$	$\pm 10\%$	$\pm 40\%$
CNI	Condition I curve number for site	0.02	0.02	−0.04	−0.17	0.01	−0.12	0.04	−0.06
CONA	Soil evaporation factor	0.00	0.00 <sup>a</sup>	0.00	0.00 <sup>a</sup>	0.00	0.00 <sup>a</sup>	0.00	0.00 <sup>a</sup>
GR	Surface litter factor	0.00	0.00	−0.04	−0.04	−0.07	−0.04	−0.03	−0.01
BD	Moist bulk density of soil layers	0.07	0.02	−0.08	−0.06	−0.10	−0.19	−0.08	−0.13
SM0	Porosity of soil layers	0.00	−0.02 <sup>b</sup>	0.09	0.06 <sup>b</sup>	<b>0.15</b>	<b>0.21<sup>b</sup></b>	0.13	0.14 <sup>b</sup>
SM3	Water content at drained upper limit (−0.033 MPa)	−0.02	0.10	<b>1.41</b>	<b>1.54</b>	<b>−0.28</b>	<b>−0.05</b>	<b>−0.34</b>	<b>−0.35</b>
SM15	Water content at lower limit (−1.5 MPa)	0.00	0.00	<b>−0.51</b>	<b>−0.64</b>	−0.04	−0.05	−0.02	0.05
SLSC	Saturated soil-hydraulic conductivity	−0.02	−0.01	−0.04	−0.03	0.03	0.01	0.06	0.01
ALB	Bare soil albedo	0.00	0.00	0.02	0.02	0.01	0.01	0.03	0.01
NIT1	Initial inorganic nitrate in upper soil layer	<b>0.79</b>	<b>0.66</b>	0.03	−0.04	0.06	0.04	0.18	0.15
NIT2	Initial inorganic nitrate in lower soil layer	0.32	0.22	0.01	0.00	0.01	0.01	0.05	0.04
RES	Initial plant litter dry matter	0.00	0.00	0.00	0.00	−0.01	0.01	0.02	0.03
DROOTS	Dead root dry matter in soil	0.00	0.00	0.00	0.00	−0.02	0.00	−0.05	−0.02
PNS <sub>1</sub>	Decomposition rate of dead root dry matter	0.00	0.00	0.00	0.00	0.04	0.00	−0.02	−0.01
PNS <sub>3</sub>	Decomposition rate of soil organic matter	0.02	0.02	0.02	0.02	0.05	0.03	0.17	0.15
KDET	Rate of nitrate denitrification	−0.01	−0.01	0.00	0.00	−0.02	0.00	−0.07	−0.04
KMANR	Mineralization rate of organic manure residue nitrogen	0.00	0.00	0.01	0.01	−0.03	0.01	−0.21	−0.04
KRESR	Mineralization rate of organic plant residue nitrogen	0.00	0.00	0.00	0.00	−0.02	0.01	0.11	0.09
LCOEF	Soil leaching coefficient	−0.14	−0.07	0.00	0.00	0.02	−0.01	0.00	−0.01
PNUNAVL	Proportion soil N unavailable to plants	<b>−0.84</b>	<b>−0.63</b>	0.11	−0.02	−0.13	−0.12	<b>−0.34</b>	<b>−0.30</b>

Values in bold indicate, by season, the two site-specific parameters to which predictions appear most sensitive (see text for explanation of *S*).

<sup>a</sup> decreased only by 25% due to model constraints.

<sup>b</sup> decreased only by 30% so it would remain larger than SM3.

the method of Pierson et al. (2001), parameters were varied individually by  $\pm 10\%$  and  $\pm 40\%$  to learn how sensitivity to a parameter varied with the magnitude of change, and a normalized sensitivity parameter was calculated for each of the two levels of variation using the following equation:

$$S = [(O_H - O_L)/O_M]/[(I_H - I_L)/I_M], \quad (1)$$

where  $I_L$  and  $I_H$  represented the lower and higher values, respectively, of the input parameter,  $I_M$  represented the mean of those values,  $O_L$  and  $O_H$  represented the corresponding output for the lower and higher input values, respectively, and  $O_M$  represented the mean of the two output values. For example, an  $S$  value of 1.0 meant that output changed in a direct and equal proportion over the range of change in input (e.g.,  $\pm 10\% = 20\%$ ), while an  $S$  value of  $-0.5$  meant that output changed only 50% as much in an inverse proportion to the change in input.

#### 2.4. Model evaluation

Using weather data from 2003, we also tested the ability of the model to predict total shoot dry matter and soil moisture content observed during three growth cycles (spring, summer, and autumn) during the second year of the DBRC grazing experiment (2003). As in simulations of 2002, the model set total shoot dry matter equal to post-graze values observed in the field at the beginning of the summer and autumn growth cycles of 2003 (8 Jul and 9 Sep), decreasing shoot dry matter of all species by the same proportion.

### 3. Results and discussion

#### 3.1. Sensitivity analysis

Sensitivity of total shoot dry matter predictions to input parameters changed with the season simulated (Tables 3 and 4). In the spring growth cycle, total shoot dry matter appeared most sensitive to parameters dealing with photosynthesis and growth rates, especially the temperatures describing the shape of photosynthetic activity ( $P_{3-5}$ ) and the proportion of substrate at which photosynthesis stops (FDBKCM). In the summer growth cycle, which occurred during a drought in 2002, it appeared most sensitive to factors influencing soil water content, such as the maximum proportion of shoot structure that photosynthesizes ( $P_{32}$ ), soil water content at the drained upper and lower limits (SM3 and SM15), and the specific leaf area ( $P_{16}$ ). Both  $P_{32}$  and  $P_{16}$  directly influenced the LAI of photosynthetic shoot structure, which determined potential transpiration. Shoot dry matter also appeared sensitive in the summer to the mean soil water potential that halves the photosynthetic rate ( $P_6$ ) and the parameter that distributed roots among soil layers ( $V_1$ ) further highlighting the importance of soil water during the drought. In the autumn growth cycle, shoot dry matter appeared most sensitive to phenological parameters such as the day of the year that senescence begins and ends (CRIT<sub>7</sub> and CRIT<sub>8</sub>); it

also showed sensitivity to the optimum temperature for photosynthesis ( $P_4$ ). For the last day of the year (day of year 365), shoot dry matter appeared most sensitive to the same three parameters ( $CRIT_7$ ,  $CRIT_8$ , and  $P_4$ ), as well as the maximum nitrogen proportion in live shoots ( $CRITN$ ) and the proportion of additional shoot death after senescence ( $P_{21}$ ). Among all seasons, shoot dry matter appeared most sensitive to optimum photosynthesis temperatures, the specific leaf area, the start and end dates of senescence, the maximum nitrogen concentration in live shoots, and the maximum shoot specific growth rate. Species-specific parameters usually had more influence on shoot dry matter than site-specific parameters.

Model sensitivity to  $\pm 40\%$  changes in most parameters varied little from sensitivity to  $\pm 10\%$  changes, suggesting a relatively linear relationship between input and output over that range. For a few parameters, such as the maximum temperature for photosynthesis ( $P_3$ ) in the summer and at the end of the year, the model appeared more sensitive to larger input changes. For other parameters the model had greater sensitivity to the smaller change, suggesting a threshold or limit to the increase or decrease (e.g., interaction between start and end dates of senescence ( $CRIT_7$  and  $CRIT_8$ ) and dates of the autumn growth cycle, interaction between the soil leaching coefficient ( $LCOEF$ ) and soil nitrate in spring). Overall, despite the substantial changes made to the structure of SPUR, dry matter production in the model remained sensitive to many of the same parameters identified in previous studies of SPUR: photosynthetic temperatures, maximum photosynthetic rate, and senescence start and end dates (MacNeil et al., 1985; Carlson and Thurrow, 1992). Like this study, an earlier study also identified the lesser importance of site-specific parameters compared to species-specific parameters (MacNeil et al., 1985).

### 3.2. Model evaluation

Model predictions of soil water content at 13 and 61 cm depths in 2003 followed observed dynamics well (Fig. 2). Though Foy et al. (1999) found SPUR predictions of soil moisture weak, our adjustments to the SPUR 2.4 hydrology submodel (especially the limitation of transpiration deficit) made soil moisture predictions acceptable for our purposes. Simulation of temperate pastures, which are much less water-limited than semi-arid rangelands, probably reduced the importance of the hydrology submodel in our simulations. Since the modified SPUR submodels predicted soil moisture content relatively well, the calibrated site-specific hydrological parameters also seemed acceptable. Consequently, we did not attempt to incorporate a recent, but more complex, enhancement of SPUR (SPUR 2000; Pierson et al., 2001) that improved predictions of rangeland hydrology by adjusting potential evapotranspiration calculations and adding the infiltration submodel from the Water Erosion Prediction Project (Flanagan and Livingston, 1995).

The model tended to underpredict spring shoot dry matter accumulation slightly but to predict summer and autumn shoot dry matter accumulation reasonably (Fig. 3). A least-squares regression of observed values of dry matter accumulation on model predictions at 22 dates during the growing season had a strong

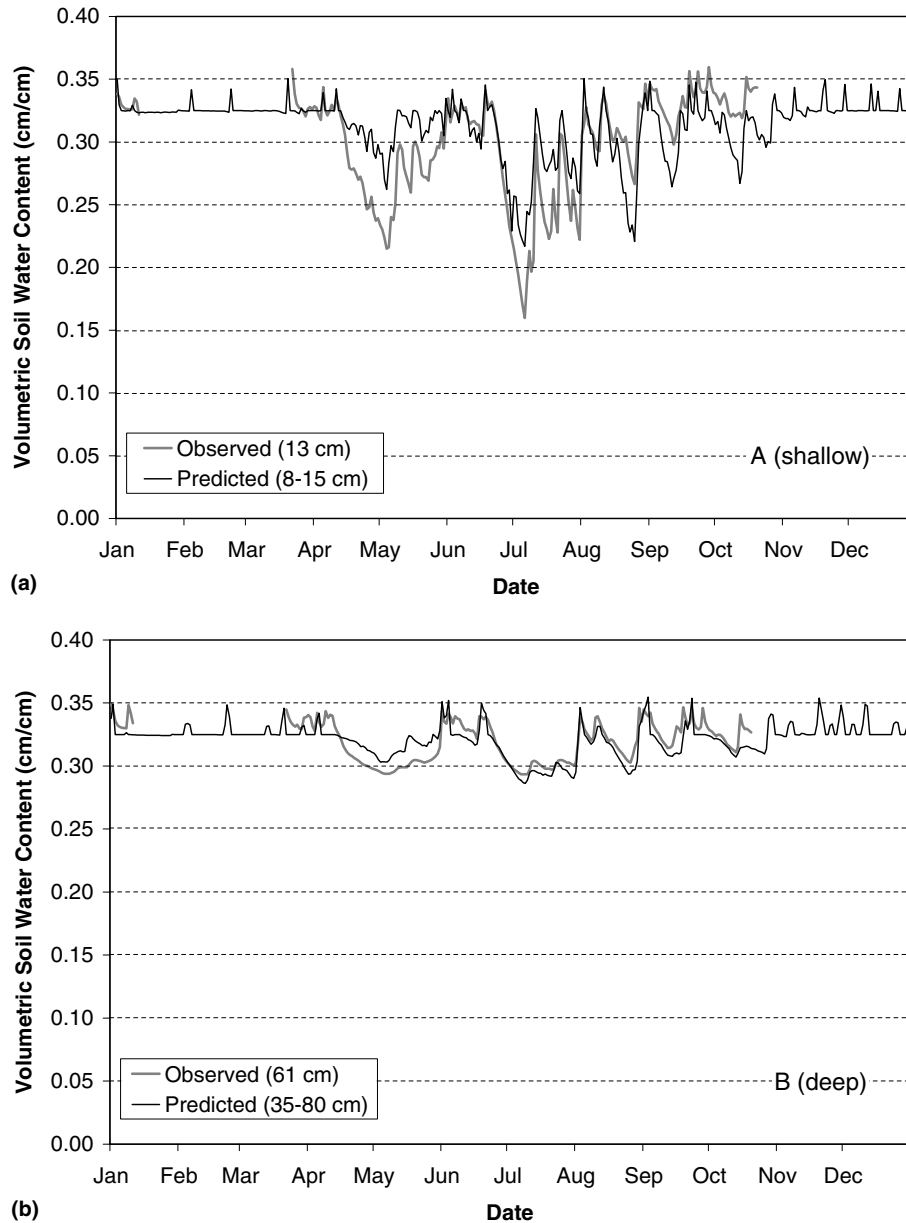


Fig. 2. Observed (a) shallow (13 cm) and (b) deep (61 cm) volumetric soil water contents in 2003 compared to model predictions.

correlation coefficient ( $r = 0.923$ ) and a slope of 0.724. The mean squared deviation (MSD) from the 1:1 line between predictions and observations (Kobayashi and Salam, 2000) equalled 581. Its square root (24.1) equalled the standard



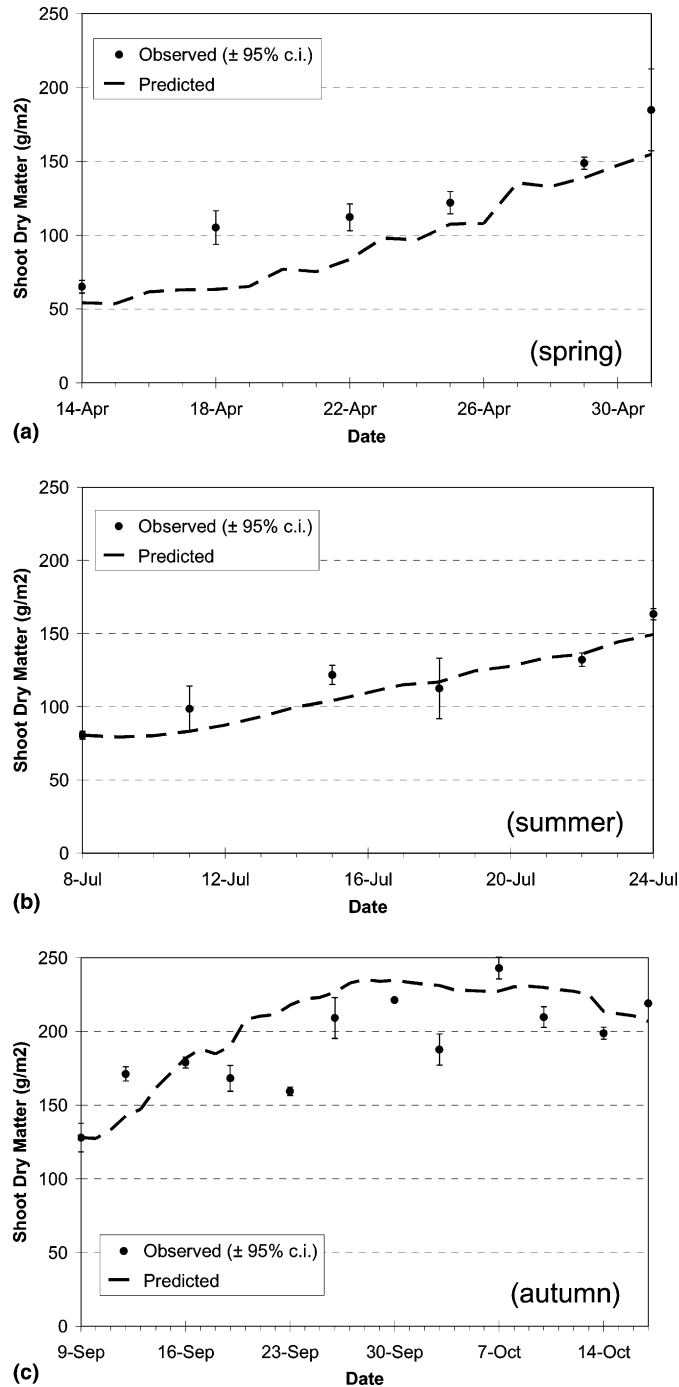


Fig. 3. Observed ( $\pm 95\%$  c.i.) total (live and dead) shoot dry matter during (a) spring, (b) summer, and (c) autumn growth cycles in 2003 compared to model predictions.

deviation of deviations around the 1:1 line (analogous to the root mean squared error (RMSE) of the regression line); as such, it served as a better indicator of the accuracy of model predictions than RMSE. Subcomponents of MSD (i.e., squared bias = 3, non-unity slope = 263, lack of correlation = 315) (Gauch et al., 2003) indicate that prediction–observation deviations were due primarily to scatter around the 1:1 line (lack of correlation), followed by a regression slope that deviated from the 1:1 line (non-unity). Thus, though the model had little mean bias (squared bias = 0.5% of MSD), it had some random prediction errors (lack of correlation = 54.2% of MSD) and systemic bias (non-unity slope = 45.2% of MSD). The systemic bias appears due to overestimation of autumn dry matter (which had relatively higher observed values) and underestimation of spring dry matter (which had relatively lower observed values).

A recent evaluation of SPUR 2.4 for cow-calf management in rangelands showed adequate prediction of live and dead herbage under moderate grazing, but overprediction under heavy grazing, mostly due to overprediction of C<sub>3</sub> wintergrass production (Teague and Foy, 2002). In our study, though predicted dry matter production appeared sensitive to certain parameters only during a single season, sensitivity among all seasons to parameters such as photosynthetic temperatures and the maximum specific growth rate increased calibration difficulty. Often, adjustments that increased predicted dry matter production to observed values in spring 2002 caused the model to overpredict previously acceptable summer and autumn dry matter predictions. Additionally, the relatively large number of parameters needed to characterize each species, many of which are rarely measured in field or laboratory experiments (e.g., proportion of photosynthate translocated to roots after senescence begins), also increased calibration difficulty.

The model had difficulty predicting botanical composition of the pasture accurately (Fig. 4). In the spring and summer growth cycles, the model tended to underpredict the proportion of white clover and dead dry matter in the pasture and overpredict the proportions of orchardgrass and weeds. In the autumn growth cycle, the model continued to underpredict the proportion of dead dry matter but reversed its previous trends, overpredicting the proportion of white clover dry matter and underpredicting the proportions of orchardgrass and weeds. Likewise, the recent evaluation of SPUR 2.4 (Teague and Foy, 2002) showed difficulties in predicting mean monthly standing crop of live and dead C<sub>4</sub> shortgrass and, under heavy grazing, C<sub>3</sub> wintergrass and C<sub>3</sub> annual grass, suggesting occasional inaccuracies in predicting botanical composition.

Inaccurate predictions of botanical composition highlight challenges in calibrating the integrated SPUR submodels due to their complex structures and interactions. Species-specific parameters, especially those involved with interactions between plants and soil water or nutrients, require additional calibration. The need to calibrate the model with field data from 2002, a drought year, may have contributed to model overestimates of orchardgrass and weed production in 2003, a wetter-than-average year. Performing sensitivity analysis of the model with data from a drought year, however, revealed the greater sensitivity of summer dry matter production to parameters influencing soil moisture during drought.

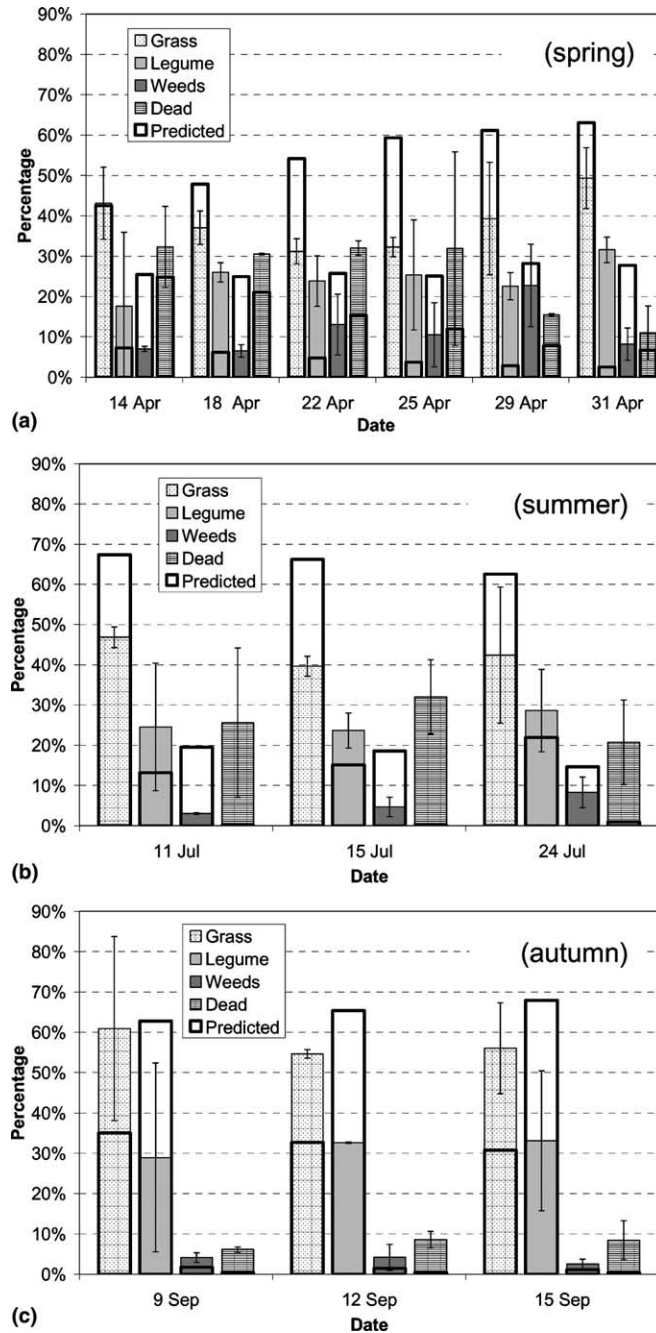


Fig. 4. Observed ( $\pm 95\%$  c.i.) botanical composition (percent grass (orchardgrass), legume (white clover), weeds, and dead dry matter) during (a) spring, (b) summer, and (c) autumn growth cycles in 2003 compared to model predictions. Shaded bars represent observed means for each component, while heavily lined open bars superimposed on shaded bars represent the corresponding predicted values.

The accuracy of model predictions also was influenced by uncertainty in the estimation of input parameters. Additional and more accurate measurements of certain input parameters would reduce input uncertainty and could improve the accuracy of model predictions (Wallach and Génard, 1998). Variation in the observed field data (e.g., shoot dry matter) that were compared to model predictions also influenced the perceived accuracy of model predictions. An analysis of the mean squared error of prediction (MSEP) would estimate the difference between model predictions and the true values of corresponding field data, not just their observed values (Wallach and Goffinet, 1989). Assuming, however, that errors in measuring the observed field data were minor compared to the errors in predicting them with the model, the previously calculated MSD serves to approximate MSEP (Gauch et al., 2003).

Despite modifications, the integrated SPUR submodels still contain assumptions and mechanisms that may limit the predictive ability of the model. Carlson and Thurrow (1992) noted that the simplifying assumption of a constant maximum root:shoot ratio ( $P_9$ ) may lead to inaccurate predictions of plant response to management practices. Another SPUR assumption maintains a 3:1 ratio of shoot:root nitrogen concentrations during the growing season, decreasing linearly to 1:1 between dates of senescence ( $CRIT_7$  and  $CRIT_8$ ). Allowing nitrogen partitioning to vary during the growing season may improve predicted nitrogen stress of plants, a strong limitation to non-legume plant growth in temperate climates. Interestingly, SPUR seems to have difficulty simulating legumes, which usually have little internal nitrogen stress to limit their growth. Without simulated nitrogen stress in the model, only temperature, moisture, and substrate proportion (added from IFSM) remain to influence growth rate. In addition, our specification of a maximum proportion of photosynthetic shoot structure, rather than explicitly represented leaf and stem dry matter, may not have captured shoot dynamics adequately. Plus, SPUR appears to contain few time lags for plant response; once temperature, moisture, and soil nitrogen conditions become favorable, plants respond instantaneously (in the same daily time-step), with little regard to previous physiological status. To improve accuracy of dry matter predictions, future efforts will focus on improving representation of root–shoot carbon and nitrogen partitioning, while explicit representation of competition for light and water among species may improve prediction of botanical composition.

Similar challenges exist for others creating ecosystem models that attempt to predict botanical composition and dry matter production among more than two species or functional groups. For example, researchers recently produced and evaluated an updated version of GRASIM that simulates multi-species pastures and includes a submodel that predicts biological nitrogen fixation (Zhai et al., 2004). The model, with parameters optimized for multi-species pastures in Pennsylvania, reasonably simulated biomass dynamics of multiple plant species, giving correlation coefficients that ranged from 0.25 to 0.98 between observed and predicted biomass of dominant species (Zhai et al., 2004). In another study, Goslee et al. (2001), using the individual-based plant model ECOTONE (Peters and Herrick, 2001), found extremely high sensitivity of botanical composition to simulated allelopathic effects of a knapweed species (*Acroptilon repens*) in Colorado rangeland. Models such as these can help

elucidate the intrinsic and extrinsic factors that influence intraspecific and interspecific plant competition for resources, which influences the yield and quality of pastures and the persistence of plant species within them.

#### 4. Conclusions

The revised SPUR submodels provide the ability to simulate the dynamics of multiple plant species or functional groups, as well as the hydrological and soil-nutrient status of pastures in temperate climates. Several modifications to SPUR resolved conceptual weaknesses in its representation of plant physiology and soil water when used to simulate temperate pastures. Further development and use of this integrated model can help researchers improve their understanding of relationships among temperate pasture system processes, identify gaps in knowledge, and prioritize future research activities. Ultimately, the integrated model could provide more accurate assessment of the influence of management strategies on pasture productivity, animal production, and economics at the whole-farm scale.

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#### References

- Blaikie, S.J., Martin, F.M., Mason, W.K., Connor, D.J., 1988. Effects of soil–water supply and temperature on the photosynthesis of white clover and paspalum in irrigated pastures. *Aust. J. Exp. Agric.* 28, 321–326.
- Bullock, J.M., Pywell, R.F., Burke, M.J.W., Walker, K.J., 2001. Restoration of biodiversity enhances agricultural production. *Ecol. Lett.* 4, 185–189.
- Bunce, J.A., 2000. Acclimation to temperature of the response of photosynthesis to increased carbon dioxide concentration in *Taraxacum officinale*. *Photosynth. Res.* 64, 89–94.
- Cannell, M.G.R., Thornley, J.H.M., 2000. Modelling the components of plant respiration: some guiding principles. *Ann. Bot.* 85, 45–54.
- Carlson, D.H., Thurow, T.L., 1992. SPUR-91: Workbook and User Guide, Report no. MP-1743. Texas A & M University, Department of Rangeland Ecology and Management in cooperation with USDA Soil Conservation Service, College Station, TX.
- Carlson, D.H., Thurow, T.L., 1996. Comprehensive evaluation of the improved SPUR model (SPUR-91). *Ecol. Model.* 85, 229–240.
- Flanagan, D.C., Livingston, S.J., 1995. WEPP User Summary. National Soil Erosion Research Laboratory, West Lafayette, IN, 131pp.
- Foy, J.K., 1993. Soil organic matter changes as a function of stocking rate and grazing system under different climate regimes for the Central Plains Experimental Range. M.S. Thesis, Colorado State University, Ft. Collins, CO, 85pp.
- Foy, J.K., Teague, W.R., Hanson, J.D., 1999. Evaluation of the upgraded SPUR model (SPUR2.4). *Ecol. Model.* 118, 149–165.

- Gastal, F., Lemaire, G., 2002. N uptake and distribution in crops: an agronomical and ecophysiological perspective. *J. Exp. Bot.* 53, 789–799.
- Gauch, H.G., Hwang, J.T.G., Fick, G.W., 2003. Model evaluation by comparison of model-based predictions and measured values. *Agron. J.* 95, 1442–1446.
- Goslee, S.C., Peters, D.P.C., Beck, K.G., 2001. Modeling invasive weeds in grasslands: the role of allelopathy in *Acroptilon repens* invasion. *Ecol. Model.* 139, 31–45.
- Hanson, J.D., Baker, B.B., Bourdon, R.M., 1992. Documentation and Users Guide for SPUR2, Report no. 1. USDA Agricultural Research Service, Great Plains Systems Research Unit, Ft. Collins, CO.
- Hanson, J.D., Skiles, J.W., 1987. Plant-component parameter estimation. In: Wight, J.R., Skiles, J.W. (Eds.), *SPUR: Documentation and User Guide*. USDA Agricultural Research Service, pp. 240–259.
- Hanson, J.D., Skiles, J.W., Parton, W.J., 1987. Plant component. In: Wight, J.R., Skiles, J.W. (Eds.), *SPUR: Documentation and User Guide*. USDA Agricultural Research Service, pp. 57–74.
- Hanson, J.D., Skiles, J.W., Parton, W.J., 1988. A multi-species model for rangeland plant communities. *Ecol. Model.* 44, 89–123.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, H., Freitas, H., Giller, P.S., Good, J., Harris, R., Höglberg, P., Huss-Danell, K., Joshi, J., Jumpponen, C., Körner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.-D., Siamantziouras, A.-S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., Lawton, J.H., 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286, 1123–1127.
- Høgh-Jensen, H., 1997. Biological nitrogen fixation in clover-ryegrass systems, Ph.D. Dissertation. The Royal Veterinary and Agricultural University, Copenhagen, Denmark, 50pp.
- Høgh-Jensen, H., Schjørring, J.K., 1997. Interactions between white clover and ryegrass under contrasting nitrogen availability: N<sub>2</sub> fixation, N fertilizer recovery, N transfer and water use efficiency. *Plant Soil* 197, 187–199.
- Johnson, I.R., Ameziane, T.E., Thornley, J.H.M., 1983. A model of grass growth. *Ann. Bot.* 51, 599–609.
- Jones, C.A., Ritchie, J.T., Kiniry, J.R., Godwin, D.C., 1986. Subroutine structure. In: Jones, C.A., Kiniry, J.R. (Eds.), *CERES-Maize: a Simulation Model of Maize Growth and Development*. Texas A&M University Press, College Station, TX, pp. 49–111.
- Jung, G.A., Baker, B.S., 1985. Orchardgrass. In: Heath, M.E., Metcalfe, D.S., Barnes, R.F. (Eds.), *Forages: the Science of Grassland Agriculture*. Iowa State University Press, Ames, IA, pp. 224–232.
- Kobayashi, K., Salam, M.U., 2000. Comparing simulated and measured values using mean squared deviation and its components. *Agron. J.* 92, 345–352.
- MacNeil, M.D., Skiles, J.W., Hanson, J.D., 1985. Sensitivity analysis of a general rangeland model. *Ecol. Model.* 29, 57–76.
- Mohtar, R.H., Buckmaster, D.R., Fales, S.L., 1997. A grazing simulation model: GRASIM. A: model development. *Trans. ASAE* 40, 1483–1493.
- Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Sci. Soc. Am. J.* 51, 1173–1179.
- Peters, D.P.C., Herrick, J.E., 2001. Modelling vegetation change and land degradation in semiarid and arid ecosystems: an integrated hierarchical approach. In: Wainwright, J., Thornes, J. (Eds.), *Land Degradation in Drylands: Current Science and Future Prospects*. *Advances in Environmental Monitoring and Modelling*, vol. 2, No. 1. Source: <http://www.kcl.ac.uk/advances>.
- Pierson, F.B., Carlson, D.H., Spaeth, K.E., 2001. A process-based hydrology submodel dynamically linked to the plant component of the simulation of production and utilization on rangelands SPUR model. *Ecol. Model.* 141, 241–260.
- Rotz, C.A., Satter, L.D., Mertens, D.R., Muck, R.E., 1999. Feeding strategy, nitrogen cycling, and profitability of dairy farms. *J. Dairy Sci.* 82, 2841–2855.
- Sanderson, M.A., Skinner, R.H., Barker, D.J., Edwards, G.R., Tracy, B.F., Wedin, D.A., 2004a. Plant species diversity and management of temperate forage and grazing land ecosystems. *Crop Sci.* 44, 1132–1144.

- Sanderson, M.A., Soder, K.J., Brzezinski, N., Muller, L.D., Skinner, R.H., Taube, F., Goslee, S.C., 2004b. Plant species diversity influences on forage production and performance of dairy cows on pasture. *Grassl. Sci. Europe* 9, 632–634.
- Shaffer, M.J., Halvorson, A.D., Pierce, F.J., 1991. Nitrate Leaching and Economic Analysis Package (NLEAP): model description and application. *Managing Nitrogen for Groundwater Quality and Farm Profitability*. Soil Science Society of America, Madison, WI, pp. 285–322.
- Stout, W.L., 1994. Evaluation of the SPUR model for grasslands of the northeastern United States. *Agron. J.* 86, 1001–1005.
- Stout, W.L., Vona, L.C., Skiles, J.W., Shaffer, J.A., Jung, G.A., Reid, R.L., 1990. Evaluating SPUR model for predicting animal gains and biomass on eastern hill land pastures. *Agric. Syst.* 34, 169–178.
- Teague, W.R., Foy, J.K., 2002. Validation of SPUR2.4 rangeland simulation model using a cow-calf field experiment. *Agric. Syst.* 74, 287–302.
- Thornley, J.H.M., 1998. *Grassland Dynamics: an Ecosystem Simulation Model*. CAB International, New York, NY, 218pp.
- Tivy, J., 1990. *Agricultural Ecology*. Longman Scientific & Technical, Harlow, England, 288pp.
- Wallach, D., Génard, M., 1998. Effect of uncertainty in input and parameter values on model prediction error. *Ecol. Model.* 105, 337–345.
- Wallach, D., Goffinet, B., 1989. Mean squared error of prediction as a criterion for evaluating and comparing system models. *Ecol. Model.* 44, 299–306.
- Wallach, D., Goffinet, B., Bergez, J.-E., Debaeke, P., Leenhardt, D., Aubertot, J.-N., 2001. Parameter estimation for crop models: a new approach and application to a corn model. *Agron. J.* 93, 757–766.
- Wu, L., McGeachan, M.B., 1999. Simulation of nitrogen uptake, fixation and leaching in a grass/white clover mixture. *Grass Forage Sci.* 54, 30–41.
- Zhai, T., Mohtar, R.H., Karsten, H.D., Carlassare, M., 2004. Modeling growth and competition of a multi-species pasture system. *Trans. ASAE* 47, 617–627.